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Shell Exchange in Hawaiian Hermit Crabs[1]

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ABSTRACT: Shell exchange behavior of intertidal Hawaiian hermit crabs was observed in the laboratory. Outcomes of 255 shell-related interactions were analyzed to test the predictive powers of two models of resource exchange. In the case of intraspecific interactions, the negotiations model (which predicts that exchanges should occur only when both crabs will gain in shell value) was superior to an aggression model of resource exchange. In the case of interspecific interactions, the negotiations model accurately predicted outcome of *Calcinus-Calcinus* interactions, but poorly predicted outcome of *Calcinus-Clibanarius* interactions.

HERMIT CRABS NEED GASTROPOD shells for protection, and one means of acquiring them is by exchange of shells with other crabs (Hazlett 1966). Shells can be a limiting resource for crabs (Hazlett 1981), and the behavior patterns associated with the exchange of this resource have often been viewed as fights (Hazlett 1967, 1972, Bach et al. 1976, Dowds and Elwood 1983, 1985). Indeed, an earlier paper on Hawaiian hermit crabs (Hazlett 1970) viewed shell fights as a mechanism of ecological competition.

The idea that exchanges of shells occur primarily when both crabs gain in resource value has been termed negotiations (Hazlett 1978), and this type of behavioral interaction can result in ecological processes that differ qualitatively from competition (Hazlett 1987, Vandermeer et al. 1985). These ecological processes can occur both intraspecifically (Abrams 1982*a*) and interspecifically (Hazlett 1983).

Because most of the results that support the negotiations model of resource exchange were obtained from observations of Caribbean species of hermit crabs, it is of interest to examine the resource exchange patterns of Pacific species to test the generality of the model. Before the development of the negotiations idea as an alternative model of resource exchange, an earlier study of Hawaiian species (Hazlett 1970) emphasized the aggressive/competitive nature of hermit crab interactions.

MATERIALS AND METHODS

Crabs used in the study were collected at a variety of locations around the island of Oahu, Hawaii. The crabs were placed in water tables at the Hawaii Institute of Marine Biology, Coconut Island, Oahu. The crabs were not experimentally treated in any way and were interacting with each other in an environment that was similar to a 0.5 × 1.5 m tide pool. Observations were made during daylight hours, using natural lighting, during the months of January through May of 1988. Crabs were periodically fed with algae and detritus on rocks placed in the water table. Species composition and the relative proportions of different species changed over the 5 months of observation as new specimens were continually added to the water table. Thus no quantitative statements about the relative amounts of inter- versus intraspecific interactions can be made.

The observer sat near the water table and continually scanned the water table for social behaviors (the results of reproductive interactions are reported elsewhere [Hazlett 1989]). A shell-related interaction was recorded when-

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ever shell rapping was seen. This rapid bringing together of shells by an initiating crab occurs only in the context of shell exchange attempts, and shell exchanges do not occur without shell rapping. Whenever shell rapping occurred (see Hazlett 1966 for description), special attention was paid to that interaction. Although attention was focused on the shell-related interaction, the rest of the water table was also scanned for additional interactions. Up to five interactions at a time could be followed; however, usually only one interaction was in progress at a time. It is important to remember that these observations were of crabs that were not manipulated in any way other than being collected and placed in a water table. Crabs that have been experimentally manipulated behave differently in shell-related interactions (Hazlett, unpublished data).

Shell-related interactions terminate in one of two ways. Either the noninitiator comes out of its shell and an exchange of shells occurs (exchange) or the initiator stops rapping behavior and walks away from the shell it was attempting to obtain (no exchange). Once the nature of the outcome of the interaction was determined by the behavior of the crabs, both crabs and their shells were removed from the water table and set aside for later measurements. After a period of observations was finished, data regarding the interactants were recorded. The species, sex, reproductive condition of females (berried or not), and size in terms of millimeters of cephalothorax length were recorded. The species of gastropod shells of the initiator and noninitiator was recorded, and the shells were placed in a 60° C drying oven for at least 48 hr. The shells were then weighed, first each shell by itself and then when filled with fine sand of known specific gravity. The latter measurement allowed subsequent calculation of the internal volume of the shells.

The desired shell size of several species of crab with regard to several species of gastropods was determined by free-access experiments (Hazlett 1970). Thirty to 60 crabs of a particular species were placed with an excess (100–200) of empty shells of a given species of gastropod for at least 48 hr. Shell sizes were chosen to cover the size range possibly used by the crabs being tested. Each crab had about 201 shells to choose from (its own and 200 empty ones) since crabs can only occupy one shell at a time. After this period, the crabs were removed and the crab and shell parameters were measured as outlined above. From these data, a regression line between crab size and shell size for each particular crab-gastropod species combination was calculated. These regressions were obtained only for the more common crab-shell combinations.

The data were then analyzed, case by case, to determine if the outcome of each interaction fit one, both, or neither of two models of resource exchange (Hazlett 1983, 1987). Although the initiating individual was usually larger than the noninitiator, either individual could be the larger crab in a given interaction. In the aggression model, it is predicted that a shell exchange will occur only when the exchange will lead to a better shell for the initiating crab and the initiator is larger. A particular shell could be better in terms of size of the shell (closer to the desired shell size as determined by the free-access experiments) or the species of shell, if there are clear interspecific preferences. The negotiations model (Hazlett 1978) predicts that shell exchanges will occur only if both participants will obtain a better shell as a result of the exchange. If only one crab (the initiator) will obtain a better resource, no exchange will occur, according to the negotiations model. Each shell-related interaction was scored as to the accuracy of each model in predicting the outcome of the interaction. The outcome of an interaction could be correctly predicted by one, both, or neither model.

After measurements of its cephalothorax, each crab was given a new shell and returned to the intertidal zone, thus limiting its data input to one interaction. This process was not followed for two species, each represented by just one individual. One of these was a single specimen of *Calcinus haigae* and the second a new species of *Calcinus* currently being described by P. A. McLaughlin.

RESULTS

For five crab species (*Clibanarius zebra, Calcinus laevimanus, Calcinus latens, Calcinus seuratic*, and *Calcinus elegans*) the relationship between crab size and desired shell volume was determined for *Trochus intextus*. Interestingly, the slope of the crab size–desired shell size relationship was essentially the same for all five species of crab (the crab species by crab size interaction term from an analysis of variance analyzing variation in shell volume chosen with crab size as a covariate; $F = 0.667$, $P = 0.616$). However, both crab size ($F = 307$; df = 4, 1; $P < 0.001$) and crab species ($F = 3.2$, $P = 0.003$) significantly affected shell volume chosen. This indicates that although the slopes are not different for the different crab species, the intercepts are different. That is, crabs the same size but of different species selected different-sized shells.

A total of 255 shell-related interactions was observed. Of these, 144 were intraspecific and 111 were between crabs of different species. Overall, the aggression model correctly predicted the outcome of the interactions 45% of the time, while the negotiations model was correct in 71.6% of the cases.

In the intraspecific cases (Table 1), the pattern of outcomes was similar in all the species observed.The aggression model was, in every case, a poorer predictor of the outcome of interactions (ranging from 25% correct for *Calcinus laevimanus* to 56% correct for *Calcinus seurati*). The negotiations model correctly predicted the outcome of interactions in between 69% (*C. laevimanus*) and 78% (*Clibanarius zebra*) of the intraspecific cases for which reasonable-sized data sets were available.

It should be noted that in the case of *Calcinus seurati* a number of cases involved females carrying eggs as the initiator ($n = 16$ out of 99 cases in which a *C. seurati* was the initiating crab). Previous studies on other species (Hazlett 1966) indicated that berried females rarely were initiators in shell exchanges.

In the case of interspecific interactions, almost all possible combinations of species as either initiator or noninitiator were observed (Table 2). There were two exceptions to this generality. Individuals of *Clibanarius zebra* rarely initiated interactions with an individual of any *Calcinus* species. A few such interactions were observed but they were indeed not common and none involved individuals of *C. laevimanus*. All four *Clibanarius*-initiated interspecific interactions resulted in no shell exchange. Second, individuals of *Calcinus seurati* were rarely the noninitiator in interspecific interactions. This may be the result of the rapid locomotory capabilities of *C. seurati*, which allow it to run away from a potential shell-related interaction initiated by slower crabs (i.e., individuals of other species).

The outcomes of all of the interspecific interactions between individuals in the genus *Calcinus* were predicted well by the negotiations model. The precentage of cases correctly predicted ranged from 100% (*C. seurati, C. haigae, C. latens*, and *C. elegans* as noninitiators) to 87% (*C. laevimanus* as noninitiator). These interactions are clearly similar in the pattern of their outcomes to the intraspecific interactions observed. However, where a *Calcinus* crab was the initiator and an individual of *Clibanarius zebra* was the noninitiator, the pattern was different. The negotiations model did not predict the outcomes well (56% correct, $n = 52$). Individuals of *C. zebra* frequently exchanged shells, especially when the initiator was *Calcinus laevimanus*, when the exchange resulted in occupation of a shell that was a poorer fit than the one previously occupied.

DISCUSSION

The results of these observations and analyses demonstrate that Pacific hermit crabs tend to follow the negotiations model of resource exchange. Crabs exchange gastropod shells when the exchange will result in a gain in shell fit for both individuals, and if the noninitiator would not gain in shell fit no exchange occurred. This pattern predominated in the intraspecific interactions of all species

TABLE 1

OUTCOME OF INTRASPECIFIC SHELL-RELATED INTERACTIONS AND SUCCESS OF TWO MODELS IN PREDICTING THE OUTCOME OF INTERACTIONS (AN INTERACTION COULD FIT THE PREDICTIONS OF ONE, BOTH, OR NEITHER MODEL)

CRAB SPECIES	*n*	% RESULTING IN EXCHANGE	% CORRECT BY AGGRESSION	% CORRECT BY NEGOTIATION
Clibanarius zebra	54	21	39	78
Calcinus seurati	63	29	56	73
Calcinus laevimanus	20	35	25	69
Others*	7	28	42	60
Overall	144	27	42	73

* *Calcinus latens* and *Calcinus elegans*.

TABLE 2

OUTCOMES OF INTERSPECIFIC SHELL-RELATED INTERACTIONS IN HAWAIIAN HERMIT CRABS

INITIATING SPECIES	SPECIES OF NONINITIATOR			
	C. zebra	*Calcinus seurati*	*C. laevimanus*	OTHER *Calcinus**
Clibanarius zebra	—	*n* = 1	*n* = 0	*n* = 3
	—	ex = 0	ex = 0	ex = 0
	—	% agg = 0	% agg = —	% agg = 33
	—	% neg = 100	% neg = —	% neg = 100
Calcinus seurati	*n* = 10	—	*n* = 21	*n* = 6
	ex = 5	—	ex = 6	ex = 2
	% agg = 50	—	% agg = 38	% agg = 67
	% neg = 50	—	% neg = 86	% neg = 100
Calcinus laevimanus	*n* = 37	*n* = 5	—	*n* = 12
	ex = 13	ex = 2	—	ex = 5
	% agg = 49	% agg = 60	—	% agg = 50
	% neg = 54	% neg = 100	—	% neg = 100
Other *Calcinus**	*n* = 5	*n* = 1	*n* = 4	*n* = 6
	ex = 1	ex = 1	ex = 1	ex = 1
	% agg = 60	% agg = 100	% agg = 50	% agg = 50
	% neg = 75	% neg = 100	% neg = 100	% neg = 100
All cases	*n* = 52	*n* = 7	*n* = 25	*n* = 27
	ex = 19	ex = 3	ex = 7	ex = 8
	% agg = 50	% agg = 57	% agg = 40	% agg = 52
	% neg = 56	% neg = 100	% neg = 87	% neg = 100

NOTE: For each combination of initiating and noninitiating species the following are given: *n* = the number of interactions observed, ex = the number of exchanges that actually occurred, % agg = the percentage of interactions correctly predicted as to outcome by the aggressive model, and % neg = the percentage of interactions correctly predicted as to outcome by the negotiations model.

* *Calcinus latens*, *C. elegans*, *C. haigae*, and *Calcinus* (undescribed sp.).

studied. As in studies on both Caribbean and European species, the outcome of about 20% of the interactions was not accurately predicted by either the negotiations or aggression model. I have suggested elsewhere (Hazlett 1987) that this may be the result of inexperience with particular shell types.

The interspecific shell exchanges fell into two quite distinct categories. The intrageneric *Calcinus* interactions were very well predicted

by the negotiations model. In almost every single case, crabs exchanged only if both participants gained in shell fit. This was the case even for species pairs that do not frequently occur in the same habitat (i.e., *Calcinus seurati* rarely would interact with other *Calcinus* species because of its supratidal distribution [Reese 1969, Wooster, 1984].

In contrast, when *Clibanarius zebra* was the noninitiator, the outcomes of interspecific interactions were poorly predicted. This is consistent with earlier observations (utilizing methodologies that could not distinguish between the aggression and negotiations models) that *Calcinus* species are dominant over *Clibanarius* species (Hazlett 1970, Bach et al. 1976, Abrams 1981, 1982*b*, Bertness 1981). However, the *Calcinus-C. zebra* result from the present study contrasts with the results from ecologically and behaviorally similar pairs in the Caribbean (Hazlett 1983). In the latter cases, *Clibanarius* species rarely initiated interactions with individuals of *Calcinus*, but as noninitiators they exchanged shells only when it resulted in a gain in shell fit. The methodological approaches were virtually identical in the two studies. It is not clear why *C. zebra* (in Hawaii) would be so strongly dominated by *Calcinus* species while *C. tricolor* and *C. antillensis* in the Caribbean are not so dominated. The extent of ecological overlap is similarly high in both pairs, and both pairs are found together over a wide range of the respective oceans. In both locations, the *Clibanarius* species is found higher in the intertidal and the *Calcinus* species has much larger chelipeds. Individuals of *Calcinus* appear to be more aggressive in both locations (Dunham 1981), but in the Caribbean interspecific interactions are best predicted by the negotiations model while they are not in the case of the Pacific pair.

If the pattern of exchange observed in the laboratory in Hawaii occurs in the field, it would at least partially explain the poorer fit of crabs to their shells previously reported for *C. zebra* compared to *Calcinus* species (Hazlett 1970). Although *Calcinus* species could, in theory, interact in either a competitive or mutualistic manner (Hazlett 1987), it seems that the interactions of *Clibanarius zebra* with other intertidal diogenids is more likely to be of a competitive nature.

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